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Review Article

Marine nematodes of Costa Rica: state of the art

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Abstract

Nematoda is the fourth most diverse animal phylum and is widely distributed. Marine nematodes are generally the most speciose group of meiofauna, yet there are relatively few studies on the taxonomy and biodiversity of free living marine nematodes. Here we present a review of the existing scientific literature and data in international databases on marine nematodes of Costa Rica. Most of the papers currently available mentioned Nematoda as the most abundant phylum in terms of the number of individuals within sand samples, nonetheless, only three publications included taxonomic data such as the description of new species or new records. Most publications are for the Pacific coast and we found only one paper for the Caribbean coast of Costa Rica. Large sections of the coasts and almost all the Exclusive Economic Zone remain unexplored in terms of nematode diversity, abundance and ecological role. Ten species, five free-living and five parasitic species, have been reported from the coasts of Costa Rica. Several reports indicate the presence of nematodes without further identification. More effort should be dedicated to the taxonomic identification of nematodes since, in addition to being the most abundant group, they can also be used as biological indicators.

Key words: Caribbean, eastern Pacific, Isla del Coco, marine biodiversity, Nematoda

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Introduction

Nematodes are the most abundant animal phylum in terms of the number of individuals, accounting for around 1% of the total animal biomass (Bar-On et al. 2018), and the fourth most speciose phylum with 25,043 described species (Zhang 2013). They are also ubiquitous and can be found in most ecosystems, even the Polar regions (Caruso et al. 2019), where they can represent several niches ranging from free-living species to plant and animal parasites. Nematodes can even be important as bioindicators of environmental quality in a broad range of natural and agro-ecosystems (Savin et al. 2015; Moura and Franzener 2017), including estuarine and marine ecosystems (de la Cruz and Vargas 1987; Geetanjali et al. 2002; Losi et al. 2013; Semprucci 2013; Ridall and Ingels 2021). The few taxonomic studies from tropical areas indicate that marine nematodes can be very diverse; for example, Armenteros et al. (2020) identified 215 species, 138 genera, 35 families, seven orders and two classes of marine nematodes in seagrass beds in Cuba.

The biodiversity of Costa Rica has been studied for a long time and some groups are relatively well known (Cortés and Wehrtmann 2009; Wehrtmann et al. 2009; Avalos 2019). However, nematological data is mainly focused on species of economic, veterinary or medical relevance whereas soil and marine nematode diversity is mostly unknown, especially free-living taxa. Several studies on Costa Rican marine ecosystems report the presence of nematodes from several environments such as beaches (Dexter 1974; Sibaja-Cordero et al. 2019), mud flats (de la Cruz and Vargas 1986, 1987; Vargas 1988, 2016; Dittmann and Vargas 2001), coral reefs (Guzmán et al. 1987), sandy bottoms (Sibaja-Cordero et al. 2016) and deep-waters (Neira et al. 2018; Gracia et al. 2020). Nonetheless, their taxonomic status is usually not assessed despite nematodes comprising up to 75% of the meiofauna of a muddy beach in the Gulf of Nicoya. Moreover, only three papers include taxonomic details of parasitic and free-living species (Cobb 1920; Hoberg et al. 1998; Oliveira et al. 2011).

In this paper we present a review of current knowledge of the marine nematodes of Costa Rica to highlight the lack of data on the diversity of the group as well as some limitations and gaps in their study and characterization.

Methods

To compile the information on marine nematodes of Costa Rica, we searched what has been published and what is recorded in international databases: OBIS (http://www.obis.org), GBIF (https://www.GBIF.org), Nemys (World Database of Nematodes http://nemys.ugent.be/) and WoRMS (World Register of Marine Species http://www.marinespecies.org/index.php). From the publications we extracted the level of taxonomic identification, sampling locality and the year. The international databases were searched using the key words “Nematoda” and “Costa Rica”. Reported localities were plotted on a map made with GMT (Wessel et al. 2013).

Results

From the 14 papers where marine nematodes of Costa Rica are mentioned, only one has information on the Caribbean coast (Table 1, Fig. 1) and all but three refer to nematodes as a group with no further identification. All ten identified species were found on the Pacific coasts, five of them being described by Cobb (1920).

The most recent description is that of the parasitic species *Echinocephalus janzeni* from a sting ray (Hoberg et al. 1998). Four additional parasitic taxa were found in stranded cetaceans, mainly dolphins (Solano-Barquero et al. 2023).

Discussion

Several taxonomical changes and occurrence reports are available for these 10 species, and a summary of their status and related literature is given below.

Free-living taxa

The following free-living nematodes were all described by Cobb (1920) from samples collected from Puntarenas, on the Pacific coast of Costa Rica. It is

Table 1. Published reports of marine nematodes of Costa Rica.

Habitat	Locality	Coordinates	Years sampled	References
Caribbean coast				
Sandy beach	Puerto Viejo, Limón	9°40'N, 82°44'W (9°39'N, 82°45'W)*	1971	Dexter 1974
Pacific coast				
Unknown	Puntarenas, Puntarenas	Unknown	Unknown	Cobb 1920
Sandy beach	Playita Blanca, Guanacaste	10°34'N, 85°42'W (10°33'N, 85°42'W)*	1971	Dexter 1974
Muddy beach	Punta Morales, Golfo de Nicoya	10°04'N, 84°58'W	1983	de la Cruz and Vargas 1986
Muddy beach	Punta Morales, Golfo de Nicoya	10°04'N, 84°58'W	1984	de la Cruz and Vargas 1987
Coral reef	Isla del Caño, Puntarenas	8°43'N, 83°52'W	1984	Guzmán et al. 1987
Muddy beach	Punta Morales, Golfo de Nicoya	10°04'N, 84°58'W	1984–1985	Vargas 1988
Parasite	Playa Panamá, Guanacaste	10°15'N, 86°00'W	1992	Hoberg et al. 1998
Parasite	Along the Pacific coast, Guanacaste and Puntarenas	Several beaches along the Pacific coast	2001–2009	Oliveira et al. 2011
OMZ**	Off the central Pacific coast, Puntarenas	Several points between 400 and 1800 m depth	2009	Neira et al. 2018
Methane seep	Off the central Pacific coast, Puntarenas	8°55.778'N, 84°18.730'W ~1,000 m depth	2010	Gracia et al. 2020
Sandy bottom	Isla del Coco, Pacific Ocean	24 sampling stations around the island	2010	Sibaja-Cordero et al. 2016
Sandy beach	Golfito, Golfo Dulce Punta Morales, Golfo de Nicoya Junquillal, Guanacaste	8°64.26'N, 83°17.40'W 10°06.30'N, 84°95.68'W 10°96.86'N, 85°68.84'W	2014–2017	Sibaja-Cordero et al. 2019

Coordinates are given as detailed in the corresponding source, corrected coordinates (*) were also available.
** OMZ = Oxygen Minimum Zone.

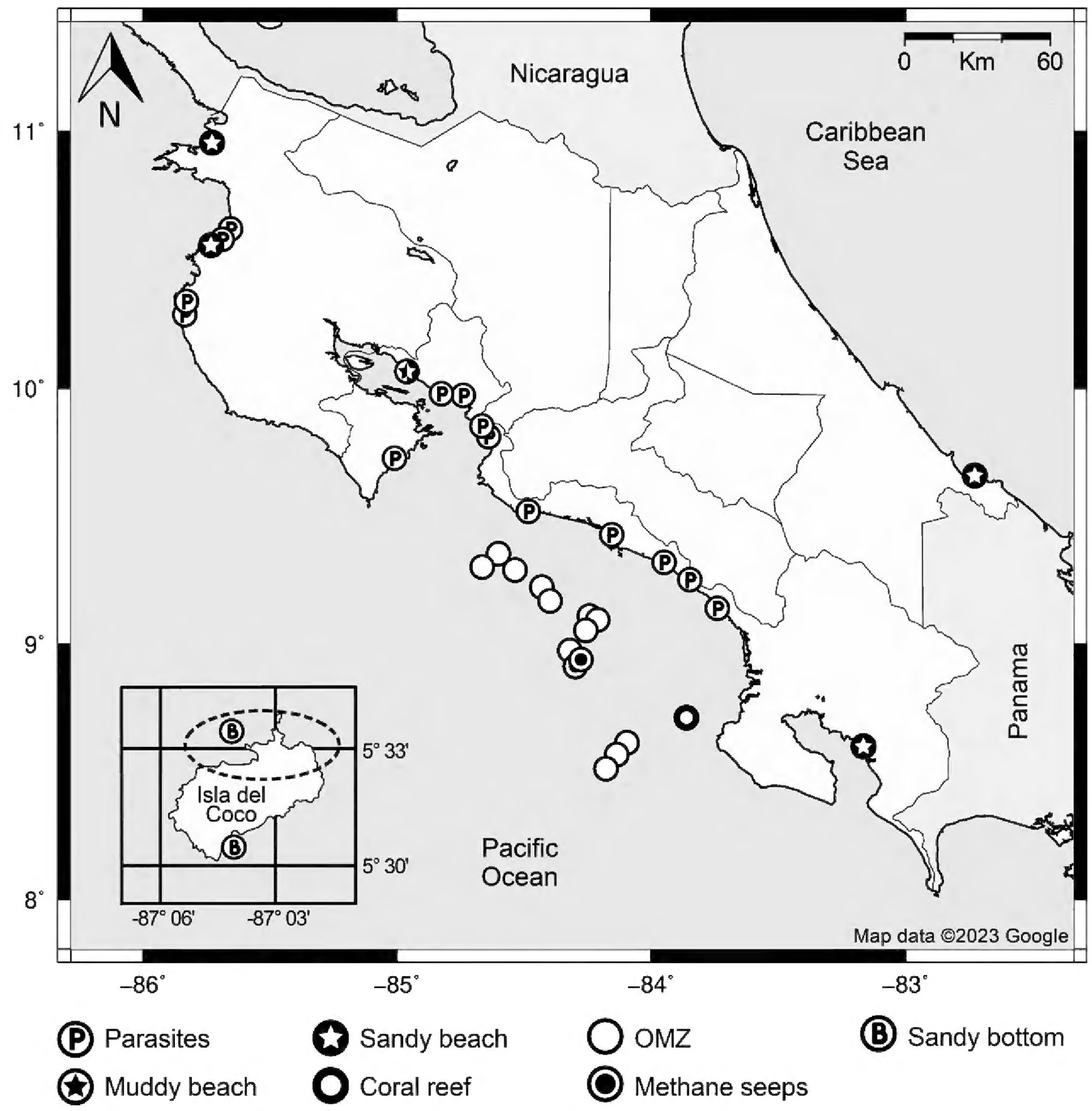

Figure 1. Sampling sites on the Caribbean and Pacific of Costa Rica where free-living and parasitic nematodes have been reported in literature. Dotted oval on the north side of Isla del Coco corresponds to more than 20 sampling points.

important to point out that the locality name is misspelled in the descriptions and should be read "Puntarenas" instead of "Punta Arenas".

Antomicron pellucidum Cobb, 1920

According to WoRMS, ten species comprise the genus *Antomicron*, the type species being *A. pellucidum*. Nonetheless, Holovachov (2012) recognizes only six valid species pointing out that several taxa in the genus were never found again; *A. pellucidum* remains valid despite the illustrations in the original description being insufficient for comparisons (Holovachov 2012). Remarkably, the specimen studied by Holovachov (2012) was found 274 m offshore at Turkey Point, Florida, Gulf of Mexico while the species was described from specimens from the Pacific coast off Costa Rica.

Hypodontolaimus punctulatus (Cobb, 1920) Filipjev 1934

= *Iotadorus punctulatus* Cobb, 1920.

WoRMS and Nemys register 27–30 species in the genus *Hypodontolaimus* but only 26 are regarded as valid by Venekey et al. (2019), including *H. punctulatus*. Three years earlier, Huang and Gao (2016) questioned the validity of *H. punctulatus* because only females were known; however, males are present in the original description (Cobb 1920) as stated by Venekey et al. (2019). No more details about *H. punctulatus* (including geographic distribution) were found.

Pseudochromadora quadripapillata Daday, 1899

= *Desmodora cephalata* (Cobb, 1920).
= *Desmodora luticola* (Timm, 1952).
= *Desmodora quadripapillata* (Daday, 1899).
= *Micromicron cephalatum* Cobb, 1920.
= *Micromicron luticola* Timm, 1952.

Pseudochromadora comprises thirteen species worldwide (WoRMS), but only five species are valid according to Muthumbi et al. (1995). *P. quadripapillata* was listed as *P. luticola* in a biodiversity survey in Brazil (Venekey et al. 2010) and reported as *M. cephalatum* from Vietnam (Gagarin and Thanh 2015). Current georeferenced records include the Caribbean coast of Belize, the Bay of Fundy on the Atlantic coast of Canada and the Maldives (GBIF). This species was reported by Cobb (1920) as a new marine taxon, however, WoRMS includes freshwater as a plausible environment. According to Verschelde et al. (2006), *P. quadripapillata* has been reported from New Guinea, Costa Rica, Brazil, two sites in USA, Nil Kamal, Bay of Bengal, Canada, Solomon Islands and Australia.

Pseudolella cephalata Cobb, 1920

Pseudolella cephalata remains valid within a dozen *Pseudolella* species (GBIF; Nemys) while Wang and Huang (2016) list fourteen species and provide a key

to 11 valid species. No further information was found for this species except for "benthos" as its functional group (Nemys) which was not mentioned in the original description. Geographic distribution data are not available.

Zygonemella striata Cobb, 1920

= *Daptonema matrona* Neres, Fonseca-Genevois, Torres, Cavalcanti, Castro, Silva, Rieger & Decraemer, 2010.

Zygonemella striata is the only species of the genus *Zygonemella*. The synonymy of *Z. striata* and *D. matrona* was settled by Cunha et al. (2013). Interestingly, there are georeferenced records of new specimens from the Atlantic coast of Brazil (OBIS, Venekey et al. 2014) while the genus was described based upon samples from the Pacific coast of Costa Rica. More recently, a metabarcoding approach of Antarctic sediments found Operational Taxonomic Units (OTUs) with BLAST identity percentages matching *Z. striata*'s sequences in more than 90%, suggesting that this species may be present in that region (Fonseca et al. 2017).

Parasitic taxa

All parasitic species were found off the Pacific coast of Costa Rica.

Anisakis spp. Dujardin, 1845

= *Conocephalus* Diesing, 1860.
= *Filocapsularia* Deslongchamps, 1824.
= *Peritrachelius* Diesing, 1851.
= *Stomachus* Goeze, 1800.

Despite the number of valid species in databases varying from six (OBIS) or 12 (Nemys; WoRMS), or up to 16 (GBIF), the most recent review on the family Anisakidae registers only 10 valid species in this genus (Ángeles-Hernández et al. 2020). There is ample information since infection of human hosts, i.e. anisakiasis, is not uncommon (Patiño and Olivera 2019).

Several unidentified species of *Anisakis* were found in the digestive tracts of stranded cetaceans: three species of dolphins — *Stenella coeruleoalba* (Meyen, 1833), pantropical spotted dolphin, *Stenella attenuata* (Gray, 1846), striped dolphin and *Stenella longirostris* (Gray, 1828), spinner dolphin— and in *Ziphius cavirostris* (Cuvier, 1823), Cuvier's beaked whale (Oliveira et al. 2011; Solano-Barquero et al. 2023). Records from freshwater fish are available (see Choc et al. 2018) but these are beyond the scope of this paper. As marine parasites, the family Anisakidae has a worldwide distribution (Ángeles-Hernández et al. 2020) as is the case for *Anisakis* spp. according to Cipriani et al. (2022).

Crassicauda anthonyi Chabaud, 1962

Thirteen species belong to the genus *Crassicauda* Leiper & Atkinson, 1914 (WoRMS). European coasts account for most of the georeferenced localities (GBIF). The specimens reported from Costa Rica were found in the kidneys

of a stranded Cuvier's beaked whale (Oliveira et al. 2011; Solano-Barquero et al. 2023), and they can be fatal according to Febronio et al. (2021). The distribution of *C. anthonyi* includes the Bay of Biscay, European waters and Costa Rican North Pacific Ocean (WoRMS); in addition, it has been reported from Australia and Brazil (Febronio et al. 2021) as well as Aguada, Aguadilla, Hatillo and Vieques Island in Puerto Rico and St. Thomas in the U.S. Virgin Islands (Colón-Llavina et al. 2009).

Echinocephalus janzeni **Hoberg, Brooks, Molina-Ureña & Erbe, 1998**

E. janzeni was described from Costa Rican and Mexican specimens collected in 1992 and 1997, respectively (Hoberg et al. 1998), and these specimens were isolated from the intestine of the sting ray *Himantura pacifica* (Beebe & Tee-Van, 1941). Hoberg et al. (1998) recognized only nine species in the genus but the number in databases ranges from ten (Nemys) to 18 (GBIF). More recently, Moravec and Justine (2021) and Saad et al. (2022) presented a key for only 12 valid species including *E. janzeni*. We also found that *E. spinosus* Müller, Adriano, Oliveira, Corrêa (2022), a parasite of freshwater stingrays, is absent from the lists and keys, probably due to its recent description.

Halocercus lagenorhynchi **Baylis & Daubney, 1925 and** ***Halocercus*** **sp.**

= *Delamurella* Gubanov in Skrjabin 1952.
= *Halocercus* (*Posthalocercus*) Delyamure in Skrjabin 1942.
= *Halocercus* (*Prohalocercus*) Delyamure in Skrjabin 1942.
= *Skrjabinalius* Delyamure, 1942.

Halocercus comprises 13 valid species, the most recent being described in 2020 (WoRMS). Costa Rican *Halocercus* sp. were collected from the lungs of pantropical spotted dolphins and spinner dolphins, while *H. lagenorhynchi* was collected from air passages and lungs of stranded pantropical spotted dolphins (Oliveira et al. 2011; Solano-Barquero et al. 2023). As a side remark, Alfaro-Shigueto et al. (2022) omitted the findings of *Halocercus lagenorhynchi* in dolphins from the Pacific Ocean by only listing the Atlantic and Indian Oceans as reported localities. Nonetheless, this omission is in a non-peer-reviewed version of the on-line posted document and the information should therefore be used cautiously. Similarly, John et al. (2023) reported an infected dolphin off the Southwest coastline of India but the publishing platform of this information is also not peer-reviewed.

Abundance and unidentified taxa

The other papers on Costa Rican marine nematodes treat them as an important group of the meiofauna with no further details. They have been reported from both coasts of Costa Rica (Cortés and Wehrtmann 2009); several studies on the Pacific coasts have been performed since the 1970s, while only one paper, Dexter (1974), presents information on the Caribbean side focused on the diversity of macroscopic infauna of sandy beaches (Table 1, Fig. 1). In the late 1980s, the studies by de la Cruz and Vargas (1986, 1987) and Vargas (1988)

on intertidal mud flat samples from the Gulf of Nicoya found that nematodes represented, respectively, 74.9%, 88.1% and 82% of the total organisms. Furthermore, the vertical distribution estimated by de la Cruz and Vargas (1987) showed that 82.7% of the nematodes were found in the top 2 cm of sediments and decreased to 5.3% at 4–9 cm depth. More recently, Sibaja-Cordero et al (2016) found that nematodes represented the second highest relative abundance (21.95%) from 24 out of 27 sampling points around Isla del Coco, totalling 3382 individuals. Unfortunately, all nematodes were treated as "Adenophorea spp. indet." and no further information on their identity was given.

Abundance can be very different according to the sampling locality, as Guzmán et al. (1987) found in sediments of a coral reef at Isla del Caño Biological Reserve, with nematodes representing 19.12%. Furthermore, the numbers can fluctuate significantly between months, and also depending on sampling methodology, equipment and preservation of specimens in diversity studies (Vargas 1988).

Neira et al. (2018) assessed the distribution of meiofauna at different depths (400 and 1800 m) off the central Pacific coast. Nematodes had an overall mean relative abundance of 79.7%, ranging from 64.97% at 1800 m to a maximum of 99.9% in the Oxygen Minimum Zone (OMZ) at 400 m. The density of nematodes in Costa Rica's OMZ (~3688 ind. 10 cm^{-2}) is the highest reported compared to other OMZs in the eastern Pacific, but in terms of species richness it was one of the lowest (Neira et al. 2018). Gracia et al. (2020) studied the meio-epifaunal organisms that colonized woodblocks deployed at Mound 12, central Pacific coast, at ~1,000 m water depth. Woodblocks were placed at active methane seeps and inactive sites nearby. In such conditions, nematodes made up to 9.8% of the individuals, being more abundant in wood located in inactive sites.

There are no data of nematodes from other marine habitats, e.g., seagrasses or coral reefs in the Caribbean of Costa Rica. Interestingly, Dexter (1974) only reported nematodes in one out of five and eight Caribbean and Pacific beaches, respectively. Similarly, Sibaja-Cordero et al. (2019) found nematodes on the Pacific coast but not on the Caribbean side after sampling 16 and 12 sandy beaches, respectively.

Conclusion

Despite decades of research on Costa Rican biodiversity (Avalos 2019) marine nematodes from Costa Rica are practically unknown. Fourteen publications have mentioned Costa Rican marine nematodes but only three present taxonomic data for ten species; undoubtedly, there are far more species.

The diversity of marine nematodes is high in the tropics, for example in Cuban marine ecosystems (Armenteros et al. 2009, 2020); they are also the most abundant taxa in methane seeps in the Gulf of Cádiz (Pape et al. 2011). Similar coastal ecosystems do exist on both coasts of Costa Rica (Cortés 2016a, b) and there are also numerous methane seeps on the Pacific coast (Sahling et al. 2008; Levin et al. 2015). Regarding parasitic nematodes of marine organisms, there must be many more in Costa Rica (Solano-Barquero et al. 2023); for example, parasitic nematodes in the Mediterranean Sea have been found in edible scallops (Marcer et al. 2020) and in sea turtles (Santoro et al. 2019) such as the loggerhead turtle *Caretta caretta* (Linnaeus, 1758); the same, or similar, species are present in Costa Rica.

It is evident that taxonomic studies should be carried out to explore the actual diversity of marine nematodes in Costa Rica. More research is needed since ecological studies have highlighted the importance of this group in marine ecosystems and the potential of nematodes as biondicators (Geetanjali et al. 2002; Semprucci and Balsamo 2012; Losi et al. 2013; Savin et al. 2015; Ridall and Ingels 2021).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

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Author contributions

ASM and JC conceived the review and searched for related data in literature and databases. ASM edited the map to plot reports. Both authors wrote the manuscript and made improvements to every version of it. Both authors read and approved the manuscript.

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Data availability

The datasets analysed during the current study are available in the following URLs: OBIS (http://www.obis.org), GBIF (https://www.GBIF.org), Nemys (World Database of Nematodes http://nemys.ugent.be/) and WoRMS (World Register of Marine Species http://www.marinespecies.org/index.php).

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